CARABIDAE (COLEOPTERA) OF AN ARABLE FIELD IN CENTRAL ALBERTA

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Sixty-three species of carabid beetles were collected in pitfall traps in an arable field in central Alberta. Data on life histories or biology are given for 26 of the more abundant species and discussed, and population densities are estimated for several of these. Six species of staphylinid beetles and 12 of spiders also taken in the study are listed. The spider species included Xysticus californicus *Keys, a first record in Canada.*

Dreiundsechzig Arten von Laufkäfern (Carabidae) wurden in Fallen auf einem Ackerland in Mittelalberta gesammelt. Angaben über die Leben oder Lebensgewohnheiten wurden für 26 der häufigeren Arten angegeben und erläutert; ausserdem wurde die Populationsdichte für verschiedene von ihnen geschätzt. Sechs Arten von Kurzflüglern und 12 Spinnenarten wurden ebenso in die Studie einbezogen und aufgeführt. Die Spinnenarten schlossen Xysticus californicus *Keys, eine Art, die zum ersten Mal in Kanada entdeckt wurde, ein.*

Larvae and adults of most species of Carabidae prey upon other insects. As part of a study of the economic importance of Carabidae as predators of cutworms, a study was made of the species inhabiting an arable field in Central Alberta. Mention is made of Staphylinidae and of spiders from the same habitat.

THE STUDY AREA

This was selected following a report of a cutworm attack on a field of barley near Calahoo, Alberta. The designation of the site is: section SW8, township 55, range 27, meridian W4, which is roughly 32 km (20 miles) northwest of Edmonton. The area is mapped as a mixture of three soils: two formed on fine-textured, stone-free lacustrine sediments (these are Mico silty clay loam, comprising 50% of the area and Maywood clay loam, comprising 20%); the other on a loam-textured, stony glacial till (this is Cooking Lake loam and comprises 30% of the area).

The species of cutworm was determined as *Euxoa ochrogaster* Guenée (Lep; Noctuidae), the red-backed cutworm.

A study area of about 0.2 hectare (0.5 acre) was used, near the centre of the field. Partly because of its smallness and partly because of agricultural practices, which inhibit growth of other than the crop plant, the area was very uniform. The duration of the study was the frost-free periods of 1967 and of 1968, from June 1967. In 1968 a crop of oats was grown in the field.

THE CLIMATE

Frost occurred from early November 1967. In 1968 thawing was during the first week of May with more or less permanent frost from the first week in October. Frost limited the movement of Carabidae severely, so that the operation of pitfall traps during frost periods was unproductive. Meteorological information was supplied by the Weather Office, International Airport, Edmonton. Maximum temperatures occurred in September 1967 (max. 33.6 C, 92.5 F), but in July 1968 (max. 31.0 C, 87.8 F). Minimum temperature of the study period was -32.3 C (-26.1 F), in January 1968. This air temperature range of 65 C (over 118 F), although modified by the field crop, must impose severe restrictions on the movement of surface active insects. Refuge from temperature extremes is provided by the ability of the adult and larval carabids to burrow into the soil. From the temperature aspect the season was more 'advanced' in 1968 than in 1967.

The rainfall patterns were similar over the two years, with July and August being the wettest months (total 120-145 mm, 5-6 inches, for the two months together) but September 1967 was an extremely dry month (0.76 mm, 0.03 inch) compared with September 1968 (37.34 mm, 1.47 inches).

METHODS

The principal means of capturing beetles was a grid of 10 x 10 unbaited pitfall traps spaced at 1 m intervals. This was in place throughout the study period except when agricultural operations (ploughing, seeding, and harvesting) were in progress, at which times it was taken up, to be replaced as soon as possible. The traps were of high impact polystyrene plastic and were 10.2 cm in height, 8.7 cm (O.D.) at top and 7.2 cm (O.D.) at base. The shape allowed stacking for transportation and the light weight also facilitated this. Individual traps which had become soiled while in use were replaced by clean traps as necessary, although the plastic resisted adherence of mud. A vinyl square 10.8 x 10.8 cm (quarter of a 9 inches x 9 inches floor tile) was supported on four small wooden stakes of length about 10 cm, at a height of about 2.5 cm above each trap to keep it dry. Insects caught in the pitfall traps were removed from the study area for identification and were not returned unless they were to be used for mark, release, and recapture studies. Those not returned were used to establish and maintain cultures, or were dissected.

Population estimates were made in a way similar to that described by Frank (1967). Released beetles had been marked by cutting a minute notch in the right elytron with spring scissors instead of marking with paint.

Larvae taken in pitfall traps were reared individually, at first in plaster of Paris blocks, later in 60 x 15 mm plastic petri dishes contained in a glass battery jar to maintain an adequate level of humidity. Entomophagous larvae were fed larvae of *Musca* or pieces of *Periplaneta*, and phytophagous larvae (species of *Amara* and of *Harpalus* would not survive for long on a diet of insects) were fed pieces of maize (corn) kernel. An identification label was attached to the inside cover of each petri dish with a smear of vaseline. Food had to be replaced daily to prevent growth of mould.

Cultures of adults were maintained on a damp peat substrate in 8 x 17.5 x 4.5 mm transparent plastic boxes and were fed in much the same way as were the larvae. Eggs and larvae, when found, were removed from these cultures and treated as were the pitfall-trapped larvae.

THE CARABIDAE

Names of the 63 species collected arranged according to Lindroth (1961), with data on those less frequently collected, are given in Table 1. Data on the more abundant species follow.

Table 1. A list of names of carabid species collected in the study area near Calahoo, Alberta, with notes, numbers, and dates for the less frequently encountered species (mature adults except where otherwise noted).

Name of species	Notes
Cicindela limbalis Klug	2 – 31.VII.1967 & 20.V.1968
Carabus maeander Fischer von Waldheim	3 – 30.VI.1967 & 17.VI.1968
Carabus taedatus Fabricius	5 – VIII-IX.1967; 11 – V-VIII.1968
Carabus serratus Say	few – VII-VIII.1967 & 1968; 1 instar III – 12.VII.1968
Calosoma calidum Fabricius	text p. 241
Notiophilus semistriatus Say	1 – 18.X.1967
Notiophilus aquaticus Linnaeus	29 – X-XI.1967; 2 – VII.1968
Loricera pilicornis Fabricius	2 – VII.1967
Patrobus lecontei Chaudoir	infrequently; 4 gravid ♀♀ – 18.VII, 24.VII, & 21.VIII.1968
Bembidion nitidum Kirby	text p. 241
Bembidion grapei Gyllenhal	3 – between X & XI. 1967
Bembidion bimaculatum Kirby	text p. 241
Bembidion rupicola Kirby	text p. 243
Bembidion obscurellum Motschoulsky	text p. 243
Bembidion nudipenne Lindroth	1 – 1967; 12 – VI.1968; 7 – VII.1968; gravid ♀ – 26.IX.1968
Bembidion rapidum LeConte	2 – VI.1968
Bembidion versicolor LeConte	text p. 243
Bembidion quadrimaculatum oppositum Say	text p. 243
Bembidion mutatum Gemminger and Harold	text p. 244
Bembidion canadianum Casey	text p. 244
Pterostichus lucublandus Say	text p. 245
Pterostichus corvus LeConte	text p. 245
Pterostichus adstrictus Eschscholtz	text p. 245
Pterostichus femoralis Kirby	1 – 30.IX.1968
Calathus ingratus Dejean	text p. 246
Synuchus impunctatus Say	few, all brachypterous; ♀ – 17.VII.1967 with 43 well-developed eggs; ♀ – 21.VIII.1967 with 40 eggs; ♀ – 21.VIII.1967 with tachinid larva parasite
Agonum quadripunctatum DeGeer	1 – 26.X.1967
Agonum retractum LeConte	1 – 18.X.1967; 2 – VI.1968
Agonum cupripenne Say	2 – 17.VII.1967 & 5.VII.1968
Agonum cupreum Dejean	text p. 246
Agonum placidum Say	text p. 246
Amara lacustris LeConte	few – VII & VIII.1967 & 1968; gravid ♀ – 3.VIII.1968
Amara torrida Panzer	text p. 246

Table 1 (continued)

Name of species	Notes
Amara latior Kirby	text p. 247
Amara apricaria Paykull	text p. 247
Amara avida Say	text p. 247
Amara obesa Say	1 gravid ♀ – 28.VIII.1967
Amara quenseli Schonherr	30; gravid ♀♀ – 28.VIII.1967 & 24.VII-30.VIII.1968; 7 parasitised each by single dipterous larva – V-VIII.1968
Amara sinuosa Casey	4 – 23.VIII & 27.IX.1968 including 2 gravid ♀♀
Amara farcta LeConte	31 – V-VIII.1968; gravid ♀♀ – V & 3.VII.1968; immature adults – 30.VIII.1968; 2 ♂♂ each with 1 parasitic dipterous larva – 10 & 20.V.1968
Amara patruelis Dejean	text p. 248
Amara laevipennis Kirby	1 – 1967; 2 – 1968, 1 immature (30.VIII)
Amara ellipsis Casey	text p. 248
Amara littoralis Mannerheim	text p. 248
Amara cupreolata Putzeys	few – 30.VI & 5.IX.1967 & VIII.1968; gravid ♀ – 12.VII.1968
Amara convexa LeConte	3
Amara pallipes Kirby	1 – X.1967; 4 – VII-VIII.1968; gravid ♀ – 24.VII.1968; 2 immature ♀♀ – 30.VIII.1968
Harpalus amputatus Say	text p. 249
Harpalus funerarius Csiki	few – VI-VIII; immature adult – 9.VIII.1968
Harpalus uteanus Casey	few – IX.1967 & VII.1968; gravid ♀ – 18.VII.1968
Harpalus pleuriticus Kirby	text p. 249
Harpalus desertus LeConte	♂ – 18.VII.1968
Harpalellus basilaris Kirby	6 – VI-VII.1968
Trichocellus cognatus Gyllenhal	text p. 249
Bradycellus lecontei Csiki	1 – 2.XI.1967
Bradycellus congener LeConte	5 – VI-VII.1968; 2 gravid ♀♀ – 26.VII.1968
Bradycellus species ?	2 ♀♀, elytra iridescent – 27.X.1967 & 23.IX.1968
Stenolophus comma Fabricius	1 – 17.VI.1968
Badister obtusus LeConte	1 – VI.1968
Chlaenius alternatus Horn	1 – 18.IX.1968
Metabletus americanus Dejean	text p. 249
Cymindis planipennis LeConte	1 – 18.X.1967
Cymindis cribricollis Dejean	♂ – 17.VII.1967; gravid ♀ – 31.VII.1968
	63 species

Calosoma calidum Fabricius

No trace of this species was seen at Calahoo in 1967, but several examples were captured in 1968, with immature adults found on 16 and 26 August. Two eggs were laid by a captive ♀ on 20 June 1968 and one of these was reared to the third instar. A few living larvae were taken in pitfall traps (between 5 July and 3 August) and reared to the adult state. The average length of each stage was: egg 4 days, instar I 5 days, instar II 8 days, instar III 14 days, pupa 8 days. The life cycle is therefore complete in 5 to 6 weeks. No evidence suggests that there is more than one generation per year or that any larvae overwinter.

Bembidion nitidum Kirby

Specimens were trapped in June, September, and October 1967, and in May-July and again in late September-October 1968. The population density was estimated for 1968 as $\leqslant 1.0/m^2$.

A final instar larva, found in a culture of adults in the laboratory, on 2 January 1968, pupated on 6 January, but became infected with a fungal growth by the middle of the following month and died. Nineteen other larvae were taken from the same culture which was replenished by the addition of newly-trapped adults, in summer 1968. These appeared between 24 and 28 May and then not again until the end of July. None was reared to the adult; one, taken as an instar I larva on 24 May, underwent ecdysis on 28 May and again on 31 May, but the instar III larva was unable to pupate successfully and died on 10 June. Of the larvae which appeared at the end of July, some had reached instar III by 19 August. An instar II larva was trapped on 23 August.

Lindroth (1963) recorded immature beetles from early August and stated that hibernation is probably imaginal i.e. that larval growth takes place in the summer. However, there seem to be two breeding periods indicated first by peaks in number or activity (i.e. pitfall trap catches) in early May and late June (Fig. 1) and second by instar I larvae produced in culture only in late May and in late July. If this interpretation is correct, the immature adults recorded by Lindroth were probably from the second generation. The larva found in culture in January 1968 was perhaps properly from the first annual generation which had been produced early because of warm temperatures in the laboratory. Likewise the number or activity peak of September-October is possibly an early manifestation of that of the following May which is interrupted by freezing temperatures. A situation in some ways the reverse of this is discussed by Mitchell (1963) where a few adults of *Trechus quadristriatus* (Schrank) (which is stated to breed in September) overwinter and breed in the following spring. The development period of the supposed second annual larval generation is not necessarily of the same length as that of the first and if a third takes place during the winter, this last would obviously be much lengthened.

Bembidion bimaculatum Kirby

Many more specimens of this species were taken in August than in any other month and it appeared to have a single peak of numbers or activity (Fig. 1). Captured ♀♀ contained eggs between the end of July and early September, when as many as 17 mature eggs were contained in the abdomen of a single ♀. Larvae were taken from a laboratory culture on 4 November 1967. Lindroth (1963) considered the larva to hibernate.

The population size was estimated at $\leqslant 0.8/m^2$ in 1968. The related species *B. sordidum* Kby. was not recognised from Calahoo.

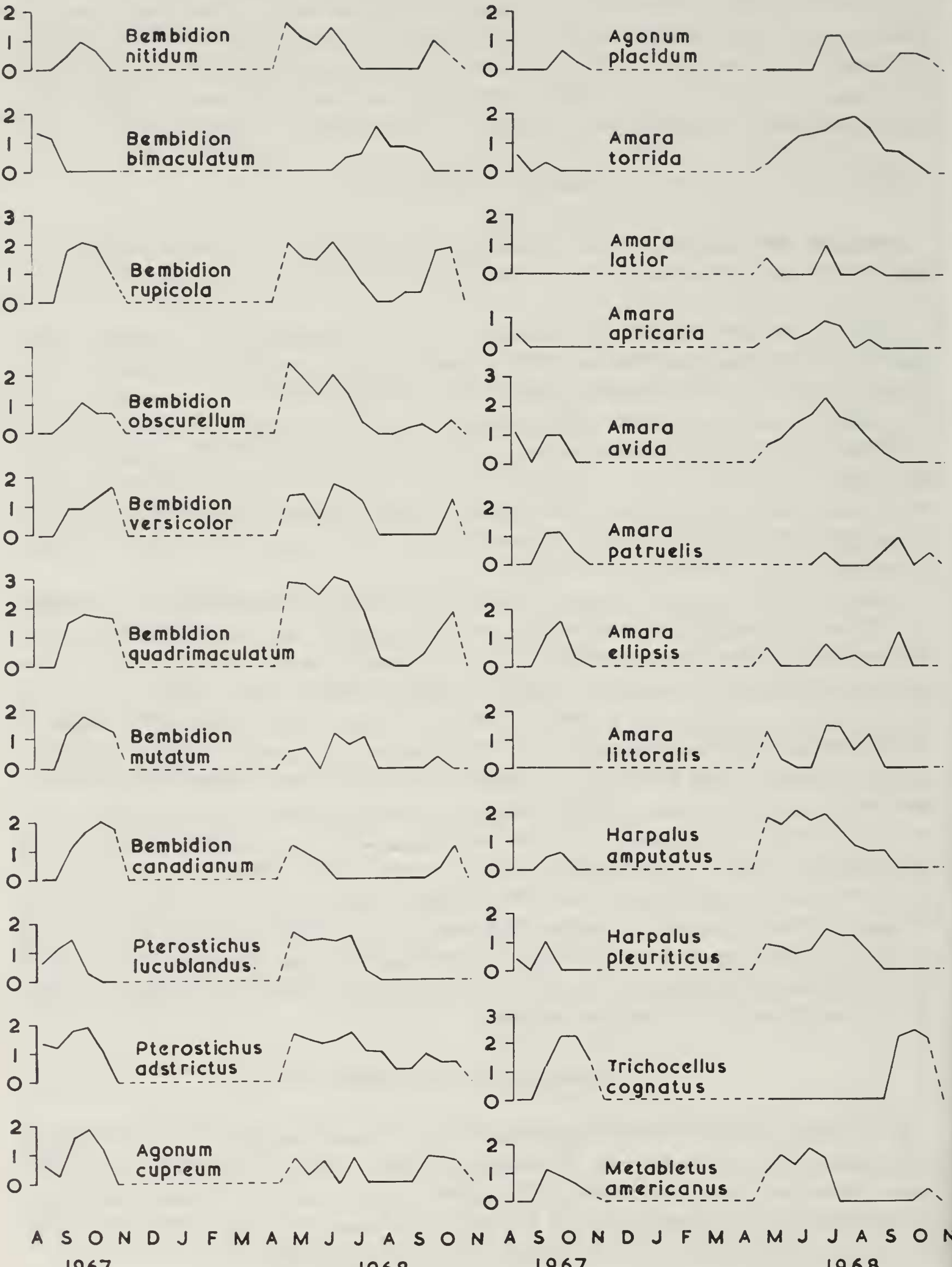

Fig. 1. Pitfall catches of Carabidae over fortnightly periods (log. scale) x time.

Bembidion rupicola Kirby

A common species at Calahoo, with an estimated population size (1968) of 2.6/m^2. Adults showed a very similar pattern of numbers or activity to that shown by *B. nitidum*, with peaks in early May, late June, and October.

Several pairs of adults were observed mating in pitfall traps on 10 May 1968. Larvae were taken from a culture of adults in the laboratory at various dates between 24 May and 10 June 1968, but none was reared successfully, so that the duration of the larval instars cannot be given. However, an instar III larva, taken at Worsley, Alberta, on 11 July 1967, pupated on 14 July and the adult emerged on 20 July. Lindroth (1963) recorded immature beetles between 22 July and 3 August and stated that adults hibernate.

If an analogy is drawn with *B. nitidum* and *B. quadrimaculatum*, below, it would seem likely that the numbers or activity peaks of early May and late June (Fig. 1) correspond to two separate breeding periods. The first generation reaches the adult state in late June. Either these adults and their parents, or both, then breed giving rise to the second generation which reaches the adult state at the end of July and beginning of August. This second generation may normally overwinter and perhaps breed in May of the following year, but a certain number of larvae may be produced in October and may overwinter.

A single instar III larva trapped at Calahoo on 11 September 1968, pupated in the laboratory on 16 September and the adult emerged on 28 September. This raises the possibility of a third generation in the year, but because of the absence of a peak in numbers or activity in early August, it seems more probable that the occurrence of this larva was exceptional.

Bembidion obscurellum Motschoulsky

Far fewer adults of this species were trapped in late 1967 than of *B. rupicola*, but the former were more numerous at the beginning of 1968. Either *B. obscurellum* adults were not influenced so greatly to activity by the warm autumn of 1967, or they survived the winter better. Population size between June and August 1968 was estimated at 3.9/m^2.

The pattern of activity appears to be identical to that of *B. rupicola*, with three peaks in numbers or activity, one in early May, the second in late June and a smaller third in October (Fig. 1). Like *B. rupicola*, adults were found mating in pitfall traps on 10 May 1968. Larvae and eggs were taken from a culture of adults on 24, 25 and 26 May and not again until 26-31 July. Lindroth (1963) recorded immature adults in late July in Alberta.

Bembidion versicolor LeConte

This species had a rather similar pattern of numbers or activity (Fig. 1) to that of *B. nitidum*. It showed a peak in early May, a second in late June and a third in November. The third peak had its beginning earlier in 1967 than in 1968. Gravid ♀♀ were taken on 19 and 26 July 1968. No larvae were obtained.

The species is somewhat hygrophilous. Specimens of the related species *B. timidum* LeConte were not collected at Calahoo.

Bembidion quadrimaculatum oppositum Say

By far the most numerous carabid at Calahoo, its population size was estimated to be 20/m^2 in 1968 with a pattern of numbers or activity (Fig. 1) similar to that of *B.*

nitidum.

Several pairs of a laboratory culture were observed mating in late May 1968. Instar III larvae were recovered from this culture on 13 June and one of these pupated on 20 June and the adult emerged on 1 July. A ♀ taken in a pitfall trap on 26 July was found to be gravid. Larvae were again taken from culture between 26 and 31 July of which one pupated on 5 August but subsequently died.

Rivard (1964) has indicated for the subspecies a breeding period extending from May until July in eastern Ontario. This was based on dissection of 72 females captured between May and November 1963, of which 24 were gravid. During most of this May-July period, according to Rivard's Fig. 1, no more than 50% of the female beetles dissected were gravid, except in early July when approximately 100% were gravid. In Rivard's Fig. 1, a line is drawn through 10 points on a graph which relate to the 24 gravid beetles and a similar number of non-gravid ones. Thus a difference of one or two gravid beetles at any date could make a large difference to the shape of the graph line.

The numbers of individuals taken in pitfall traps at Calahoo (Fig. 1) are based upon the summation of pitfall trap catches over fortnightly periods. The number taken in early May was 924; in late May 769; in early June 294; in late June 1234; in early July 872 and in late July a mere 66. Unless the substantial drop in numbers in early June and substantial increase in late June are related to breeding activity they are difficult to account for; the explanation is hardly to be sought in direct temperature or rainfall variation effects.

If no significant drop in numbers occurs, but merely a period of quiescence, then the second peak must represent a resumption of breeding activity by the same generation of adults. Thus a single generation would have two temporally (at least partially) separated breeding periods.

If a real drop in numbers occurs, then the second peak must be associated with an increase in the adult population by the metamorphosis of pupae – but the continuance of breeding activity after this date is not disputed – and this suggests true bivoltinism. On this basis, because adults of this new generation must outnumber adults of the previous generation by at least four to one (Fig. 1) in late June and thereafter, then no more than 20% of trapped females should be gravid from late June onwards, if there is no bivoltinism. Rivard found 100% of females captured to be gravid only in early July.

The evidence points to the existence of two breeding periods at Calahoo. Several other species of *Bembidion* show a very similar pattern of numbers or activity.

Bembidion mutatum Gemminger and Harold

Less numerous than the similar *B. quadrimaculatum*. The numbers trapped were small particularly in 1968, but indicate numbers or activity peaks (Fig. 1) similar to those of the above species, perhaps slightly delayed. A gravid ♀ was captured on 9 August 1968.

Bembidion canadianum Casey

As frequently trapped in late 1967 as *B. rupicola*, this species was only as numerous in 1968 as *B. mutatum*. The numbers taken in pitfall traps decreased from May 1968 until June, after which there was no activity until October (Fig. 1). The absence of a second summer peak in 1968 may indicate that the species is univoltine, if meaning can be inferred from the small numbers of individuals trapped.

Pterostichus lucublandus Say

The population size of this species was estimated at $\leqslant 0.7/m^2$ in the study area in 1968. The adults were active only during May-July of 1968, but in the milder autumn of 1967 there was another peak of numbers or activity in late September (Fig. 1). Approximately equal numbers were caught during each half-month period between early May and early July and there is no evidence to suggest that there are two activity peaks with the corollary of bivoltinism. Rivard (1964) also arrived at this conclusion of univoltinism for this species and his Fig. 1 indicated that the breeding period extends from May into September in eastern Ontario.

Females dissected on 20 May 1968 and 17 July 1967 contained large eggs. Mating of pairs caught in pitfall traps was observed on 21 May 1968 as well as in laboratory cultures during the last week of May. Eggs were produced by these cultures from 23 May until 5 June and from 8-16 July. The egg stage lasted 4-7 days, instar I 6-7 days, instar II 6-11 days, instar III 14-21 days and the pupa 8-10 days. Towards the end of July and in early August larvae were taken in pitfall traps frequently and one of these was reared to produce an adult on 23 August (pupal stage 7 days). Immature adults were taken in pitfall traps on 5 September 1968.

Larvae (apparently instar III) were described briefly by Schaupp (1881), one of which pupated on 26 August and the adult emerged on 5 September; another pupated on 18 August and the adult emerged on 29 August.

Pterostichus corvus LeConte

Not a single example of this species was taken in the study area in 1967, but 16 were taken in May-July 1968. By analogy with the related *P. lucublandus*, the population size may have been of the order of $0.07/m^2$ in 1968.

Eggs were obtained from a laboratory culture on 30 June, 14, 15 and 26 July and 3 August 1968. The average duration of each stage was as follows: egg 6 days, instar I 6 days, instar II 6 days, instar III 16 days, pupa 7 days.

Because of the small numbers trapped it is not possible to specify the breeding period or periods with any certainty. The northernmost locality given by Lindroth (1966) for the occurrence of this species in Alberta is Morin, some 150 miles SSE of Calahoo.

Pterostichus adstrictus Eschscholtz

More than twice as numerous at Calahoo as *P. lucublandus* (estimated population size in 1968 $1.8/m^2$), but apparently with a very similar life cycle. The second numbers or activity peak of late September 1967 shown by *P. lucublandus* was even more marked in this species and was repeated to some extent the following year (Fig. 1). There was a very slight diminution in numbers trapped from late May until June.

Gravid ♀♀ were found as early as 10 May and as late as 17 July, while immature adults were trapped from 21 August until 5 September. Adults in a laboratory culture produced eggs between 23 May and 26 July and the resultant larvae were reared in the same manner as those of *P. lucublandus*. The egg stage lasted 4-8 days, instar I larva 4-6 days, instar II larva 4 days, instar III 17-18 days and pupa 6-7 days. Adults reared from instar III larvae taken in pitfall traps emerged at the end of July and beginning of August.

The related *P. pennsylvanicus* LeC., although abundant at George Lake, Alberta, a marshy, wooded locality little more than 16 km (10 miles) NNW of Calahoo, was never found in the study area.

Calathus ingratus Dejean

A few individuals only were taken, in June-August of both 1967 and 1968; the normal habitat is wooded localities.

Two ♀♀ (with very reduced wings) were trapped on 17 July 1967, one of which contained eight large eggs, the other five. Another ♀, taken on 24 July 1968, was also gravid. A (macropterous) ♀, taken on 21 August 1967, contained no eggs, neither did brachypterous ♀♀ taken at Scandia and at Tofield, Alberta in April 1968.

Agonum cupreum Dejean

Estimated to have a population size of $1.0/m^2$ in 1968 at Calahoo, this species seemed to be less abundant than during the previous year. All examples from Calahoo, in which the wings were examined, proved to be macropterous.

None of the ♀♀ caught at various states between 21 April (1968) and 17 July (1967) contained mature eggs (though one contained the pupa of a parasitic hymenopteron), but a ♀ taken on 21 August (1967) contained (only) two eggs, perhaps indicating the approaching end of the breeding season. An instar III larva, trapped on 30 August 1968, pupated on 15 September and the adult emerged on 21 September. An immature adult was taken in a pitfall trap on 16 September 1968. A pair was observed in copula, in the laboratory, on 20 November 1967. Lindroth (1966) recorded immature adults at the end of July and in August.

The graph of numbers or activity (Fig. 1) is difficult to interpret and it may be that there is a single breeding period extending from May into July, but numbers trapped are too small for certainty. The September-October peak possibly represents early incidence of the activity of the following year. If breeding occurs from May to July, immature adults would be expected from late July until late September. The apparent decline in numbers between 1967 and 1968 might be the result of unsuccessful overwintering possibly as a result of the high and perhaps untimely level of activity in late 1967.

Agonum placidum Say

Less frequently captured in 1967 than was *A. cupreum*, the situation was reversed in 1968, when *A. placidum* was more often captured and its population size was estimated at $\leqslant 1.5/m^2$.

Females with eggs were taken on 17 July 1967, the maximum number of eggs recorded per ♀ being 20. Of 20 ♀♀ captured on 14 April 1968 at Scandia, Alberta, none contained eggs, but one contained two nematode parasites. Eight instar III larvae caught between 23 August and 9 September 1968 produced adults between 4 Sept. and 17 Sept., the average time for the pupal stage being 6 days.

A numbers or activity peak in July is well marked in this species (Fig. 1) and there is some evidence of a minor peak in the year (October 1967 and September-October 1968). The breeding period seemed to be restricted to July in 1968 at Calahoo. Rivard (1964) found gravid ♀♀ between June and September in eastern Ontario. Lindroth (1966) quoted records of gravid ♀♀ from June to August in southern Ontario.

Amara torrida Panzer

Lindroth (1968) wrote that the habitat of this species was similar to that of *Pterostichus* *adstrictus*. Certainly both species were common at Calahoo. The population density of *A. torrida* was estimated by the mark, release and recapture technique as $\leqslant 0.6/m^2$ in 1968. In the same year, numbers taken in pitfall traps gradually rose to a single peak in early August and then declined more rapidly (Fig. 1).

Gravid ♀♀ were trapped in 1967 on 17 July, 21 August, 24 August and 1 September, while in 1968 gravid ♀♀ were taken on 19 July and 9 August, but ♀♀ trapped on 20 May and 30 September were not gravid. The maximum number of eggs contained by a single ♀ was 20 (24 August 1967). Pairs were observed in copula on 6 August 1967 and 16 August 1968. A pitfall trap emptied on 21 August 1968 contained a single adult ♀ *A. torrida* together with two eggs (no other beetles present) which, unfortunately, did not prove to be viable. Five eggs were removed from a culture of adults in the laboratory, between 30 July and 2 August 1968, but these too were not viable. An immature adult was trapped on 17 July 1968.

This bears out the suggestion by Lindroth (1968) of larval hibernation and indicates a lengthy larval growth period. The single peak in numbers trapped, in early August, may well indicate the coincidence of the peak of the breeding period with the peak period of emergence of the new generation of adults.

Adults, each with a single parasitic dipterous larva, were captured on 10 May 1968 (1 example); 20 May 1968 (1 example); 9 August 1968 (3 examples). A male captured on 9 August 1968 was the host of a nematode.

Amara latior Kirby

Only a few individuals of this species were trapped in either year at Calahoo, the greatest number appearing in early July (Fig. 1). A gravid ♀ was taken on 5 September 1967. A larva, taken from soil on 11 July 1967 at Worsley, Alberta, pupated the same day and the adult emerged on 17 July. Lindroth (1968) recorded gravid ♀♀ in September and October in Ontario, while Rivard (1964) recorded others during August-October in eastern Ontario.

Amara apricaria Paykull

This species was commoner at Calahoo than species of *Amara* previously discussed, but numbers trapped were still too low to allow interpretation of the pattern of numbers or activity (Fig. 1). A single gravid ♀ was taken on 17 July 1968. The larva was described briefly by Schiødte (1867) but the date of capture was not given.

An individual parasitised by a dipterous larva was captured on 10 May 1968.

Amara avida Say

This species was apparently commoner at Calahoo in 1968 than was *A. torrida* ($\leqslant 0.9/m^2$) and like that species with a single peak in numbers or activity (Fig. 1). The peak, however, occurred in early July, a month earlier than the *A. torrida* peak. Some evidence of a second peak in September-October was seen in 1967 but not in 1968.

Gravid ♀♀ were taken on 17 July, 21 August and 24 August 1967 and 9 August 1968. As many as 11 eggs were dissected from a single ♀. Several eggs were laid singly by a ♀ in a laboratory culture on 3 August 1968 and some of these hatched between 9 and 12 August, but none of the resultant larvae survived instar I. A single immature individual was taken among 17 mature adults on 10 July 1968. Lindroth (1968) noticed immature adults in June in British Columbia and Alberta.

Two individuals, each parasitised by a dipterous larva, were captured on 9 August 1968.

Amara patruelis Dejean

Specimens of this species were most frequently taken in late September and early October. Two gravid ♀♀ were taken at Calahoo on 17 July 1967 and two others on 21 April 1968 at Mill Creek, Edmonton. A pair was found in copula on 6 June 1968 and an immature adult was taken in a pitfall trap on 16 August 1968. Lindroth (1968) described *A. patruelis* as "a pronounced spring species" and stated that adults hibernate. It appears as if the larvae have a summer development period in contrast to the foregoing species of the subgenera *Curtonotus* (*Amara aulica* group Lth.) e.g. *A. torrida*, and *Bradytus* (*Amara apricaria* group Lth.) e.g. *A. avida*, but the pattern of numbers or activity (Fig. 1) is difficult to interpret because of the small numbers trapped.

Three ♂♂, the first captured on 20 May 1968, the others on 11 September 1968, each contained a single parasitic dipterous larva.

Amara ellipsis Casey

Not uncommon at Calahoo. The greatest number of individuals to be taken in a two-week period was in early October 1967 and a peak at this time of year was repeated in 1968 (Fig. 1). This late-year peak is a possible forerunner of the small peak of early May. There appears to be a second peak in July. There is similarity in this to the condition shown in the *Bembidion* species and on the basis of this and the following evidence two breeding periods per year are suggested.

An overwintering ♀, hand collected on 3 April 1968, contained eggs which were not fully developed. Pitfall trapped ♀♀ yielded eggs on 10 May and on 3 and 15 July 1968; none was trapped between the middle of May and the end of June; no ♀ trapped later in the year than July was gravid. An adult emerged successfully on 19 July 1967 from a pupa which had been collected as a larva on 22 June, the date of pupation being 7 July. An immature adult was taken at Calahoo on 24 July 1968. Lindroth (1969) found immature adults at the end of July.

Three ♂♂ captured on 26 July 1968, 21 August and 30 September each contained a single parasitic dipterous larva.

Amara littoralis Mannerheim

Present and active in largest numbers in July at Calahoo, the commonest species of subgenus *Amara* (*Amara lunicollis* group Lth.). It seems to have a life cycle similar to that of *A. ellipsis*, with a peak in numbers or activity (Fig. 1) in early May and a second one in July. A decline in numbers trapped in early August is not accounted for unless the peak of late August is the result of the emergence of adults of the second generation. Two breeding periods per year are suggested.

Dissected ♀♀ contained eggs on 10 May and on 20 May 1968; none was trapped thereafter until early July. In the latter month ♀♀ contained eggs on 3, 10, 12, 15, 18, 24, 26 and 31 July, but not thereafter. Lindroth (1968) found immature adults in July and at the begining of August.

A ♀ taken on 17 July 1967 contained a larva of an unidentified tachinid, which occupied about half the volume of the host's abdomen. The empty chorion of the tachinid egg lay under the right elytron of the host. Four ♂♂, captured on 24 July 1968, 31 July (2 examples) and 3 August each contained a single parasitic dipterous larva.

Harpalus amputatus Say

According to Lindroth (1968) a xerophilous species, the most abundant of the large carabids at Calahoo in 1968, when its population size was estimated at $4.2/m^2$. The pattern of numbers or activity probably indicates a single peak in early June (1968) and extending from May until July, with slight fluctuation. A slight autumnal peak was seen in 1967 (Fig. 1), but the species was not trapped in that year until early September.

Dissected ♀♀ contained eggs on 8 May 1968, 17 July 1967, 9 August 1968 and 21 August 1967. Unfortunately no females captured in June 1968 were put aside for dissection, but all were used to establish cultures or in population estimations. The presence of gravid ♀♀ in June would have established the existence of a single breeding period as indicated by the pitfall trap captures.

Harpalus pleuriticus Kirby

The population size of this species at Calahoo in 1968 was of the order of $1.0/m^2$. The species is thus not only of smaller size but was of smaller population size than *H. amputatus*. It reached the zenith of what may be a single extensive peak in numbers or activity in July (Fig. 1). If this is, in fact, a single peak, then the breeding period may extend from May until August, as seems to be indicated with *H. amputatus*. An autumnal peak was seen in late September 1967.

Dissected ♀♀ contained mature eggs on 17 July 1967, 12, 15, 17, 18, 19 and 24 July and 9 August 1968, but not thereafter and not in May 1968. As with *H. amputatus*, no ♀♀ captured in June were set aside for dissection. A pair was observed mating in a laboratory culture on 8 July 1968. Immature adults were taken in pitfall traps on 18 and 24 July, 9 and 16 August 1968.

Adults captured on the following dates in 1968 contained parasitic dipterous larvae: 20 May (1 example); 9 July (1 example); 24 July (2 examples each with 2 parasites); 9 August (1 example with 2 parasites).

Trichocellus cognatus Gyllenhal

The adults of this species were taken at Calahoo only in late September-November, when large numbers (387 during October 1967, 465 during October 1968) were caught in pitfall traps. Freezing interfered with assessment of population size.

A pair was found mating in a pitfall trap on 2 October 1968. Lindroth (1968) stated that immature beetles are abundant from mid-July to the end of August, but this was not so at Calahoo. Larvae were taken from culture between 1 and 17 October 1968. Oviposition might well take place in October and November when temperatures allow, and larvae may overwinter.

Metabletus americanus Dejean

Adults of the species were present and active in May to mid-July and late September to November only (Fig. 1). None was captured between mid-July and late September, but a ♀ taken on 19 July 1968 was gravid. In the laboratory six instar I larvae were taken from a culture of adults between 10 and 18 July 1968, but none was reared successfully. Several instar I larvae were taken from culture on 20 November 1968, of which two underwent ecdysis to instar II on 5 December.

There was a decline in pitfall trap captures in early June, similar to that of some *Bembidion* species, so that two generations per year may be indicated. Some larvae may be produced in May and early June.

Other Arthropods

The following species of Staphylinidae were captured in the study area: *Leptacinus batychrus* Gyll., *Philonthus occidentalis* Horn, *P. concinnus* Grav., *P. furvus* Nordm., *Quedius spelaeus* Horn, *Tachyporus* sp. The third, fourth, and fifth of these were trapped only occasionally.

Spiders taken in the study area were: *Trochosa terricola* Thor., *Pardosa groenlandica* (Thor.), *P. mackenziana* Keys, *P. moesta* Banks, *Pardosa* sp. nr. *saxatilis* (Htz.), *Pardosa* sp. of *metlakatla* complex, *Gnaphosa* sp. nr. *muscorum* (Koch), *G. parvula* Banks, *Micaria* sp. nr. *alberta* Gertsch, *Xysticus californicus* Keys (1 ♀, 21 June 1968, first Canadian record), *Paraphidippus marginatus* (Walck.). *Pardosa groenlandica* was the most frequently trapped of these.

DISCUSSION

Life cycles

Perhaps more ecological studies of Carabidae have been made than of any other family of Coleoptera, but the volume of knowledge of their life cycles is slender.

Rivard (1964) concluded that for 13 species studied in eastern Ontario, each had only a single generation per year, based on occurrence of mature eggs in the ovaries of adult ♀♀. He classified them into two major groups, spring breeders and autumn breeders, with a small third group overlapping the two periods. Greenslade (1965) arrived at similar conclusions in a study of 26 species of Carabidae in England, based on observations of activity periods of adults and larvae through numbers of individuals caught in pitfall traps and the association of these activity periods with breeding activity. However, Heydemann (1963) considered a number of species of carabids in maritime Germany to have more than one breeding period per annum. He cited some species of *Bembidion* and observed that (apparently in respect of insects in general) while carnivorous forms are mostly univoltine, saprophagous forms are frequently bivoltine or polyvoltine.

Rivard's (1964) assumption that the breeding periods are coincident with the presence of mature eggs in [a high percentage of] ♀♀, with perhaps a 2-3 weeks delay between the maturity of the eggs and the onset of oviposition, is doubtless a good approximation for the population as a whole; but no allowance is made for periods of inactivity e.g. if gravid ♀♀ are inactive over the winter before oviposition. Nor is distinction made between different generations present in the population. Thus if the premise be expanded (beyond Rivard's statements) one is led to infer that adult generation I breeds, producing eggs, larval instars, pupae and thus the resultant adult generation II. The fate of adult generation I is ignored, but possibly a considerable number of adults of generation I may survive and may breed again (at a time not necessarily coincident with the breeding period of generation II). This possibility is higher in species of lower reproductive potential or lower survival rate. The survival of these adults depends upon the combined effects of parasitism (including disease), predation, inter- and intraspecific competition, climatic factors and 'natural senescence'.

Lack of information on 'natural senescence' is a result of the difficulty of observing individuals in the field over long periods of time. Conditions in the laboratory must produce anomalous results. No individual beetle in the present study survived in the laboratory for much more than 1 year. However, an adult ♂ and ♀ of *Omophron americanum* Dejean (for which Rivard (1964) gives the breeding period as May to June) were captured at Chappice Lake, Alberta, on 29 May 1967, along with five other adults, and survived in captivity until May 1969. These individuals must have been produced, as eggs, not later than the summer before capture (on Rivard's evidence) and so their total life span was at least 3 years. The 'culture' of seven adults produced eggs in June 1967 (the resultant larvae subsequently died) but none thereafter. This, however, is no proof that the normal life span approaches (or exceeds) 3 years, nor that each generation of adults breeds only once. It merely shows that adults of generation I could still form part of the population at the breeding period of adults of generation II and even of generation III.

Breeding periodicity in different parts of the geographical range of a species may differ and may or may not be directly influenced by climatic conditions. Heydemann (1963) (following Lindroth, 1945) remarked upon the different percentages of species with a summer larval growth period or with a winter larval growth period between habitats with a maritime climate and with a continental climate. The implication was that in a harsher (continental) climate, a greater percentage of species has a winter larval growth period.

Populations

The principal interest of the present study lies in the observed dominance of Carabidae among the larger soil-surface inhabiting insects of the study area and in the large number of species apparently coexisting in an apparently very uniform habitat.

On the assumption that there is at least some similarity of requirements between the *Bembidion* species, then there must be interspecific competition (Odum, 1959). If population size is taken as a measure of success in this competition, then *B. quadrimaculatum*, with a population size about double that of all other *Bembidion* species combined, must be seen as the most successful species. Similarity of requirements may not be unconnected with accepted taxonomic relationship. Nine of the 11 species belonging to different species groups of *Bembidion* (Lindroth, 1963) where there might be expected to be greater differences in requirements, but *B. rupicola* and *B. obscurellum* belong to the same species group, as do *B. quadrimaculatum* and *B. mutatum*. *Bembidion rupicola* and *B. obscurellum* were of comparable abundance in the study area in 1968, not so with *B. quadrimaculatum* and *B. mutatum*.

Few genera of Carabidae have been recorded in the literature as having restricted food preferences. It is to be expected that those species which were not merely stragglers into the area would have some food-chain relationship to the crop plant. Carabids might eat the crop plant or its seeds or stages of its decomposition, or they might be predators of other animals which do so.

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